

REPRODUCTIVE ECOLOGY OF BLACK-TAILED PRAIRIE DOGS IN MONTANA

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ABSTRACT.—Reproductive ecology of black-tailed prairie dogs (*Cynomys ludovicianus*) was studied on the Charles M. Russell National Wildlife Refuge in northeastern Montana (1978–1980 and 1985). Breeding took place from early March through early April in most years. Persistent snow cover and below normal temperatures in February and March of 1978 delayed the start of breeding. Litter size averaged 4.4 but varied significantly among years. Average yearly litter size was correlated ($r^2 = 0.986$) with summer (June–September) precipitation prior to the breeding season. Largest average yearly litter size (5.0) followed record precipitation, while the smallest average yearly litter size (3.8) followed extreme drought. More than half the yearling females failed to breed while 88% of the females two years and older bred. Testes weights were greatest early in the breeding season and regressed rapidly during April.

Black-tailed prairie dogs (*Cynomys ludovicianus*) occur throughout the Great Plains from southern Canada to Texas within an area of great climatic variation. Such climatic variation may be expected to influence timing of breeding and possibly reproductive potential of prairie dogs. Various aspects of prairie dog reproductive ecology have been studied over a wide geographic region (Wade 1928, Anthony and Foreman 1951, Anthony 1953, King 1955, Koford 1958, Davis 1966, Tileston and Lechleitner 1966, Foreman 1968, Kerwin 1972, Stockrahm 1979, Garrett et al. 1982, Hoogland 1982a, b). Although many of these studies are of one reproductive season or of a single colony, some variation in timing of breeding and number of young is apparent. Breeding in prairie dogs begins as early as late January in Oklahoma (Anthony and Foreman 1951) and as late as mid-March in North Dakota (Stockrahm 1979). Timing of breeding in prairie dogs could not be altered by manipulating temperature and photoperiod in a laboratory (Foreman 1968). Females come into estrus for one day only (Hoogland 1982b), and their gestation period is estimated between 32 and 35 days (Anthony and Foreman 1951, Hoogland 1986). Reports of average *in-utero* litter size have ranged from 4.0 (Smith 1967) to 5.2 (Tyler 1968). My study examined timing of breeding and number of young produced by black-tailed prairie dogs in Montana and sought to determine whether environmental variables might influence these parameters.

METHODS

Prairie dogs were collected at six colonies by shooting in spring of each year from 1978 to 1980 and again in 1985 on the Charles M. Russell National Wildlife Refuge in northeastern Montana (108°30'W, 47°45'N). Collections were timed to obtain pregnant females or females shortly postpartum. Some presampling in March and early April was needed to establish the onset of breeding in 1978 and 1979. The majority of prairie dogs was collected during the second and third weeks of April except in 1978 when many individuals were collected in May.

Sex, weight, and total length were recorded for each prairie dog. Lower mandibles were examined and assigned to one of three age groups based on wear of molariform teeth. These groups and criteria for classification were as follows: (1) light wear, cusps showing little or no wear; Stockrahm (1979) found this wear pattern to be characteristic of yearlings (one to two years old); (2) moderate wear, cusps showing definite wear but still very distinct; and (3) great wear, cusps worn enough to be indistinct. According to Stockrahm (1979), considerable overlap occurs in tooth wear between age classes of prairie dogs over two years; thus, the tooth-wear classes are considered only general indications of age. Numbers of embryos or uterine scars were recorded for each necropsied female. A crown-rump measurement was taken for all embryos from 1978 through 1980 but only for

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TABLE 1. Average crown-rump measurements (mm) and percentage of lactating females by week of collection during April 1978, and the years 1979, 1980, and 1985 combined.

Week	1978			N	1979, 1980, 1985			
	Crown-Rump		Percent lactating		Crown-Rump		Percent lactating	N
	Mean	SD			Mean	SD		
1-7					<5		0	2
8-14					27.6	15.8	8	60
15-21	12.0	10.0	0	17	39.9	21.2	23	13
22-28					46.4	12.5	68	22

TABLE 2. Summary of reproductive parameters for female prairie dogs collected on the Charles M. Russell National Wildlife Refuge, Montana.

Year	N	Percent breeding	Breeding females		All females	
			\bar{X} Embryos	SD	\bar{X} Embryos	SD
1978	47	63	4.4	1.2	2.7	2.3
1979	58	67	5.0	1.4	3.6	2.6
1980	46	74	3.8	0.8	2.8	1.8
1985	39	67	4.1	1.0	2.8	2.2
Total	190	67	4.4	1.2	3.0	2.3

a single embryo of each litter in 1985. Testes were weighed to the nearest 0.1 g for animals collected from 1978 through 1980.

A one-way ANOVA was used to test for variation of litter sizes among years, litter sizes among tooth-wear classes, and weights of males and females among years. Chi-square test of homogeneity was used to test for differences in proportions of breeding females among years and among tooth-wear classes. Differences in weights and lengths between males and females were tested for significance with a Student's t-test. Iterative correlation coefficients were calculated to determine the time period prior to breeding that precipitation most closely correlated with yearly average litter size. Similar calculations were also made to determine the relationship of body weight with precipitation for male prairie dogs collected in April. Females were excluded from this analysis because weights of embryos were not subtracted from their body weight.

RESULTS

A total of 367 prairie dogs (198 females, 169 males, $P > 0.10$, $X^2 = 2.292$, 1 d.f.) was collected between 11 March and 27 May. Lactating females were collected as early as 17, 13, and 14 April in 1979, 1980, and 1985, respectively. In 1978 no lactating females were collected up to 21 April, but collections were not resumed until 13 May, at which time lactating

females predominated in the collection. Small embryos (less than 5 mm crown-rump) were noted in the collection as late as 19 April 1978, 17 April 1979, 13 April 1980 and 1985. These data suggest that breeding started as early as the second week of March and continued into early April. Breeding appeared to be delayed in 1978 (Table 1). Average crown-rump measurements were smaller for embryos taken during the third week of April in 1978 compared to other years.

The first detected emergence dates for young were 11, 2, and 1 June for 1978, 1979, and 1980, respectively. No comparable observations were available for 1985. An average of 44 days elapsed between earliest parturition date and first emergence date for these years. In 1977 I observed young above ground on 24 May, and S. Olson (personal communication) reported young up on 14 May in 1981, suggesting that breeding may have taken place even earlier during those two years. Variation in timing of breeding among years appeared to be related to temperature and snow cover during February and March. These two months in 1977 and 1981 were extremely mild, with only sporadic snow cover and mean temperatures around 2 C (U.S. Dept. of Commerce, Roy 24 NE). In contrast, total snowfall in the winter of 1978 exceeded 2 m, snow remained on the ground until early April, and the mean temperature was -5 C for those two months. Although mean temperature during February and March 1979 was similar to 1978,

TABLE 3. Comparison of female reproductive parameters by tooth-wear class together with percentage wear-class distribution by year for 181 females.

Tooth-wear class	Percent breeding	Breeding ♀♀		All ♀♀		Wear-class distribution (%)			
		\bar{X} Embryos	SD	\bar{X} Embryos	SD	1978	1979	1980	1985
Light	40	4.7	1.2	1.9	2.4	53	50	44	21
Moderate	85	4.4	1.1	3.8	1.9	30	26	40	56
Great	94	4.2	1.3	3.6	1.9	16	24	16	23

TABLE 4. Percentage of pregnant females examined by year with one or more resorbed embryos together with percentage of embryos resorbed.

Year	N	Percent pregnant resorbing embryos	Percent resorbed embryos
1978	20	30	6.2
1979	21	24	4.6
1980	28	21	5.6
1985	26	23	7.1
Total	95	24	5.9

snowfall was less and the snow melted off earlier; 1980 and 1985 were intermediate to these extremes.

Approximately two-thirds of all females collected had bred. The distribution of breeding females among years was homogeneous ($P > 0.75$, $X^2 = 1.169$, 3 d.f.) (Table 2). Litter size averaged 4.4 ($SD \pm 1.2$, range 1–8) but varied among years ($P < 0.005$, $F = 7.4$, 127 d.f.) (Table 2). Average yearly litter size ranged from 5.0 in 1979 to 3.8 in 1980. Record precipitation occurred in 1978 (57.1 cm), while drought conditions existed on the study area in 1979 and 1980 (27.6 and 22.2 cm for 1979 and 1980, respectively, U.S. Dept. of Commerce, Roy 24 NE). Average litter size was best correlated with summer (June–September) precipitation of the previous year ($r^2 = 0.986$) but showed little correlation with late-fall/winter (November–March) precipitation ($r^2 = 0.004$). Number of embryos produced by all females averaged 3.0 and showed less variation among years than did average yearly litter size (embryos/breeding female).

The distribution of breeding females was not homogeneous among tooth-wear classes ($P < 0.005$, $X^2 = 48.620$, 2 d.f.) (Table 3). Only 40% of the females showing light tooth wear had bred. Among the females showing great tooth wear, 94% had bred. Average litter size did not vary ($P > 0.25$, $F = 0.9$, 119 d.f.) among tooth-wear classes, although there was a tendency for younger animals to have larger

litters. However, because of low pregnancy rate, the average number of embryos per female in the light tooth-wear class was only about half that of the other two wear classes.

Evidence of post-implantation mortality (resorption) was found each year. Resorbing embryos were found in nearly a quarter of the pregnant females (Table 4), and 5.9% of the embryos were lost. Of the 23 pregnant females found to be resorbing embryos, only two were resorbing more than one. In 1985 one female was resorbing all three embryos, and another was resorbing two of three embryos.

Average total length of males ($\bar{X} = 383.7$, $SD \pm 26.3$ mm) was greater ($P < 0.001$, $t = 5.966$, 356 d.f.) than that for females ($\bar{X} = 369.0$, $SD \pm 20.4$ mm). However, no difference was noted ($P > 0.50$, $t = 0.415$, 283 d.f.) in average weight of females ($\bar{X} = 810.8$, $SD \pm 145.0$ g) and males ($\bar{X} = 803.5$, $SD \pm 146.4$ g) collected during April. This may be accounted for by the fact that many females were pregnant at the time of collection. Weights of both females and males taken during April varied among years (females, $P < 0.05$, $F = 3.1$, 166 d.f.; males, $P > 0.05$, $F = 2.4$, 117 d.f.). Weights of males were most closely correlated ($r^2 = 0.627$) with precipitation from June through October of the previous year.

Average testes weight was greatest during March ($\bar{X} = 3.45$, $SD \pm 2.32$ g, $N = 12$) and declined through April ($\bar{X} = 0.59$, $SD \pm 0.42$ g, $N = 93$) and May ($\bar{X} = 0.38$, $SD \pm 0.26$ g, $N = 18$). Of the five male prairie dogs collected during the month of March that were assigned to the light tooth-wear class, only two had testes weights exceeding 1.0 g. Testes weights of older males collected during this month averaged 5.0 g, suggesting that many younger males may not participate in breeding. Testes of nearly all males collected in April were held abdominally.

DISCUSSION

Timing of breeding in prairie dogs has been variously reported to take place from January through March and appears to occur later with increasing latitude (Johnson 1927, Wade 1928, Anthony and Foreman 1951, King 1955, Koford 1958, Davis 1966, Tileston and Lechleitner 1966, Tyler 1968, Stockrahm 1979). Breeding took place over an extended period from early March to early April during this study. King (1955) and Tileston and Lechleitner (1966) noted that breeding occurred over a one- to two-week period. Although Foreman (1968) found that timing of breeding in female black-tailed prairie dogs could not be altered by manipulating temperature and photoperiod, it was apparent in my study that prairie dogs bred later in 1978 as a result of persistent snow cover during March of that year. Time between birth and emergence of young has been estimated at 56 days by Anthony and Foreman (1951), 45 days by King (1955), 32 to 39 days by Tileston and Lechleitner (1966), and 43.4 days by Hoogland (1986).

Litter size varied considerably among years and appeared to be influenced by precipitation from the previous year, which may also influence body weight of prairie dogs in April. Reproductive failure has been reported to occur in Townsend's ground squirrels (*Spermophilus townsendii*) under drought conditions in Idaho (BLM, U.S. Dept. Interior 1979). Reports of average *in-utero* litter size range from 4.0 to 5.2 (Johnson 1927, Wade 1928, Anthony and Foreman 1951, Koford 1958, Tileston and Lechleitner 1966, Tyler 1968) with no apparent geographical trend. The influence of yearly climatic conditions on litter size may account for this.

Despite the varying climatic conditions during this study and the resulting wide range in average litter size among years, the proportion of females breeding among years remained fairly constant with about two-thirds of the females breeding each year. Wade (1928) reported breeding in 74% of 68 female prairie dogs, and Anthony and Foreman (1951) found 73% of 15 wild-caught females to have bred. My data show that only 40% of the light tooth-wear class (i.e., yearlings) females had bred, whereas most of the females in the two older age classes had bred. King (1955)

reported no breeding by yearling females, and Tileston and Lechleitner (1966) found only one breeding yearling female. During another segment of my study involving live trapping and marking (Knowles 1982), I did not document breeding of yearlings in 27 cases in two colonies over two breeding seasons. However, Koford (1958) reported about one-third of the yearling females he collected in Colorado had bred. Stockrahm (1979) found the majority of yearlings in two colonies bred, but in two other colonies very few bred. Garrett et al. (1982) found breeding in yearlings to vary between colonies and years. Evidently breeding in yearling females is highly variable.

Resorption of embryos was a common occurrence each year. Despite some variation among years in both percent of females resorbing embryos and the percent post-implantation mortality, this did not appear to be related to environmental factors. Anthony and Foreman (1951) found evidence of resorption in 3 of 13 (23%) pregnant females and suggested that resorption in prairie dogs may be common.

Testes of most males were in regression at least two weeks before the breeding season terminated. Anthony (1953) found peak testes weight to correspond with the beginning of estrus in females and that regression of accessory sex glands lagged behind the testes, suggesting that males are capable of breeding as long as mobile sperm are present. My data indicated that many yearling males may not attain sexual maturity. Anthony (1953) found that young raised in a laboratory attained sexual maturity a month after older adults. Yearling males were reported not to participate in breeding in a study conducted by Hoogland (1982a).

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